MENDELIAN INHERITANCE OF FECUNDITY IN THE DOMESTIC FOWL, AND AVERAGE FLOCK PRODUCTION [1]

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IN 1912 I showed,[2] from extensive experimental data that, in certain breeds of domestic poultry, winter egg producing ability is inherited in a strictly Mendelian manner. It was pointed out that there was much evidence indicating that winter production was, on the whole, a rather reliable index of total fecundity capacity. As was to be expected, the novelty of the results presented in the papers referred to led to their criticism from various points of view, including that of the practical poultryman. Most of these criticisms have been based upon some misunderstanding of the nature of the results themselves. Others, and particularly those of the poultry press, have apparently been based on a purely conservative instinct to resist the intrusion of any new idea which seems to threaten those solid personal and editorial assets of (reputed) infallibility and "safe and sane" judgment.

It has seemed to the writer more likely to conduce to the advancement of knowledge in this field if he went steadily about collecting more and more concrete objective evidence rather than engaging in polemic disputations with everyone whose opinion in regard to the validity or interpretation of the earlier results chanced to differ from his own. As a result of this policy there has accumulated a large mass of additional experimental data confirming and extending the results of the earlier work.

[1] Papers from the Biological Laboratory of the Maine Agricultural Experiment Station, No. 81.

[2] Pearl, R., "The Mode of Inheritance of Fecundity in the Domestic Fowl," *Jour. Exper. Zool.*, Vol. 13, pp. 153–268, 1912. *Cf.* also "The Mendelian Inheritance of Fecundity in the Domestic Fowl," AMER. NAT., Vol. XLVI, pp. 697–711, 1912.

This material will be published as opportunity offers.

It is the purpose of the present paper to record certain facts which are pertinent to a general consideration of the problem of inheritance of fecundity, but at the same time do not fall in the direct line of the experimental inquiry. They are matters, in other words, which are essentially by-products of the investigation but still have a more or less important bearing on the interpretation, in a broad sense, of the whole.

I. The Seasonal Distribution of a Flock Egg Production under a Mendelian System of Breeding as compared with Simple Mass Selection

The mean egg production per bird in the different months of the laying year has been given by Pearl and Surface[3] in an earlier paper. Those results are based on the weighted mean production of the flocks of Barred Plymouth Rocks at the Maine Agricultural Experiment Station during the ten years that a system of mass-selection was followed in breeding for egg production.

It is an obvious deduction from the results of the Mendelian experiments recorded in the earlier papers already referred to, that by their application it should be possible to modify the average production of a flock over a rather wide range, the modification being of a fixed and permanent character under any definite conditions of environment and breeding. To many practical poultrymen the only test of the validity of the conclusions reached which has any significance, is that of average flock production. It is obvious that from a technically critical point of view such a test has, of itself, relatively small value in helping to judge of the correctness of a Mendelian interpretation. At the same time it is clear that if one takes a flock of poultry of mixed genetic constitution in respect of fecundity and aims to preserve in his breeding only animals carrying both the factors L_1 and L_2 necessary for high

[3] Pearl, R., and Surface, F. M., "A Biometrical Study of Egg Production in the Domestic Fowl." II. Seasonal Distribution of Egg Production," U. S. Dept. of Agr., B. A. I. Bull. 110, Pt. II, pp. 81–170, 1911.

production, there ought to result a marked and immediate improvement in average flock production no matter what the size of the flock.

This, as a matter of fact, is exactly what has been done in the breeding of the flock of Barred Plymouth Rocks at the Maine Station for several years past. No attempt has been made to propagate low fecundity strains, after it had once been demonstrated that this could be done. In the work since 1912 the experimental aims have been such as not to be at variance with the practical one of getting the most eggs with the least trouble and expense, so far as has concerned the Barred Plymouth Rock stock. Consequently in making the matings from which the foundation Barred Plymouth Rock stock was being maintained I have each year endeavored to keep a number of different blood lines comparatively pure for the factors L_1 and L_2, and then intercross these lines with one another.

The results have been highly successful from a practical point of view. This is indicated by the figures shown in Table I and graphically in Fig. 1. These compare the mean egg production per bird month by month under the old system of mass-selection and under the new system of breeding which recognizes the Mendelian inheritance of fecundity with sex-linkage of the factor on which high production depends. The figures for the new system are those of the laying year 1913–14. In the laying year 1912–13 the flock had not yet attained any considerable degree of homogeneity in respect of fecundity factors since up to and including the preceding year low producing genetic combinations had been deliberately propagated and therefore an average which included all birds in the flock would be manifestly unfair as a test of the practical worth on a large scale of the new systems of breeding. The laying year 1913–14 is then the first completed year on which records are available for a fair test of the Mendelian plan on a total flock scale.

The Barred Rock flock of the year 1913–14 included 192 birds which completed the year's work. A number of other birds (about 20) began the year but died before its

completion. These 192 birds were divided among three flocks of 125 each, the other birds in each flock being cross-breds of various sorts.

It is possible to compare these 1913–14 flock with the old records during nine months of the year only. The reason for this is found in the fact that the trap-nesting season is, under the present system of management, brought to a close with August. Furthermore a record is now kept of the laying of the pullets in October at the beginning of the year, whereas formerly the season's records did not begin until November 1. This comparison is made in Table I. Also in this table the production for 1913–14 is compared with the *best* single year during the mass selection experiment, when anything approaching a corresponding number of birds were included,[4] and for which all environmental conditions may be regarded as approximately normal.[5] The single year records which come nearest to fulfilling all the conditions for a fair comparison with 1913–14 are those for the 100-bird pens in the laying year 1905–06. There were two such pens and 182 birds survived through the year. There was one small environmental accident in that year which reduced the production in May somewhat.[6] There were adverse environmental influences in 1913 probably quite as effective in reducing production as anything that operated in 1905–06. The seasonal conditions, size of flock, etc., were all fairly closely comparable with those obtaining in 1913–14. At that time (1905–06) the flock had been under continuous mass selection for eight years.

There are a number of difficulties in the way of making a comparison between any single year now, and the "best

[4] The absolutely best single year under mass selection was 1901–02. That year there were only 48 birds for which records are available. These were in several respects a special lot, and can not fairly be compared with large flocks kept under ordinary flock conditions. Cf. Pearl and Surface, *loc cit.*

[5] *Cf.* Pearl, R., and Surface, F. M., "A Biometrical Study of Egg Production in the Domestic Fowl. I. Variation in Annual Egg Production," U. S. Dept. Agr., B. A. I. Bull. 110, Pt. I, pp. 1–80, 1909, for an account of the environmental difficulties in certain of the earlier years.

[6] See Pearl and Surface, *loc. cit.*, p. 18.

year'' made under the mass-selection system. In the first place in order to make the comparison at all fair the flocks in which the birds were kept when the records were made must be of approximately the same size. It has been conclusively demonstrated by earlier work in the laboratory that egg production becomes reduced as flock size increases. It would be idle to compare the results now where the birds run in flocks of 125 to 150 birds per pen with the ''best'' of those prior to 1904, when the flocks were never larger than 50 birds each and were sometimes smaller. This restricts single year comparisons then to the period after 1904.

In the second place, if we take the year when the total production was highest, as the ''best'' year, we shall find, in practically every case, that some particular month or months of this year will fall below the average for that month or months. There are then two alternatives, either, on the one hand, to take for comparison with a single year now that year under the old system of breeding which, on the whole, is the best and then make allowances for disturbing factors in particular months, or, on the other hand, to compare a single year now, month by month, with an artificial year's record made up by picking out the best record of each individual month regardless of the year in which it occurred or of the size of flock. The second of these comparisons is obviously artificial, since it is continued high production month after month in the *same* laying year which is important. It is of interest, however, to see the results of the comparison on both bases. These comparisons are made in Table I.

The best single year 100-bird pen record in the earlier period is, as already pointed out, that for 1905–06, having regard to the months here compared (November to July, inclusive). The 100-bird pen of 1904–05 made a better record during the summer than the corresponding pens of 1905–06, but fall considerably below in winter production. In 1905–06 there was an environmental accident

TABLE I

MONTHLY DISTRIBUTION OF MEAN EGG PRODUCTION PER BIRD UNDER DIFFERENT BREEDING SYSTEMS

Month	Weighted Mean Under Mass Selection	Best Comparable Year to 1913–14 of Similar-sized Flocks Under Mass Selection (1905–06 100-bird Pens)	Best Month in Any Year of Mass Selection, Any Size Flock	Year 1913–14
November.	4.63	5.38	6.45 (1904–05, 100-bird flock)	*10.76*
December.	8.91	9.91	12.02 (1901–02, only 48 birds in small flocks)	*14.19*
January...	11.71	13.27	15.21 (1901–02, only 48 birds in small flocks)	*13.88*
February..	10.87	13.39	14.46 (1905–06, 50-bird flocks)	*13.37*
March....	16.11	17.33	18.29 (1905–06, 50-bird flocks)	*19.22*
April.....	15.85	16.48[7]	18.50 (1901–02, only 48 birds in small flocks)	*18.44*
May.....	13.92	——[8]	17.02 (1902–03, 147 birds in small flocks)	*16.88*
June.....	12.46	13.47[7]	16.88 (1901–02, only 48 birds in small flocks)	*14.56*
July.....	10.87	10.49[8]	14.90 (1901–02, only 48 birds in small flocks)	*14.52*

(overfeeding of green food) in the latter part of April. This adversely affected the May production. The 100-bird pens were more affected than the 50-bird pens. Consequently, in order to give every possible advantage to the earlier period of the work, I have taken the 50-bird pen averages for April, June and July and have graphically interpolated the figure for May in the diagram.

The data in Table I are set forth graphically in Fig. 1.

From the table and the diagram the following points are to be noted:

1. It is apparent that the laying in the part of the laying year covered by the statistics was distinctly better in 1913–14 than either the weighted mean of the whole period of mass selection, or than in the best comparable year of the earlier period.

2. The difference is somewhat more pronounced in respect of winter production (*i. e.*, the laying prior to March 1) than for any other cycle. Under the earlier plan of breeding the average winter production was 36.12 eggs. This production corresponds reasonably closely to the division point at 30 eggs between genetically high and

[7] Average from 50-bird pens of same year (1905–06). See text.

[8] Average omitted because of abnormal conditions. See text.

genetically mediocre winter producers which was used in the Mendelian analysis. In the year 1905–06 the mean winter production was 41.95 eggs. In 1913–14 the pro-

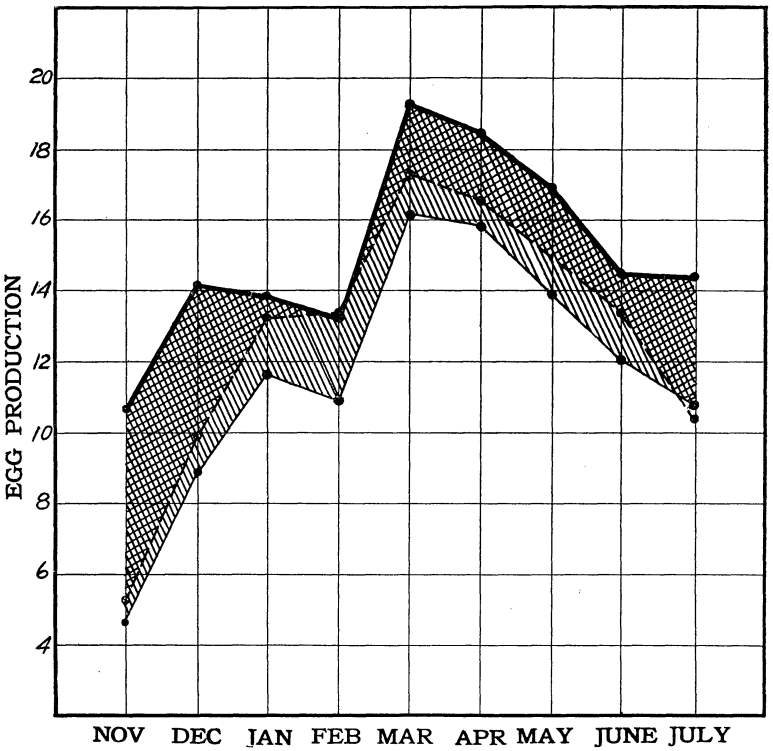

FIG. 1. Diagram comparing mean monthly egg production under different systems of breeding. The light continuous line gives the weighted means for the earlier years, the heavy continuous line the means for 1913–14, and the dotted line the means for 1905–06 100-bird pens. The cross-hatched area in comparison with the unruled area indicates in the increase of the 1913–14 averages over the earlier figures.

duction in the corresponding months was 51.20 eggs per bird.

3. It was shown by Pearl and Surface[9] that, on the average, a flock of hens produces 81.73 per cent. of their total annual yield between November 1 and August 1. Applying this figure to the 1913–14 nine-month total of 135.82 eggs, we get for the probable production of this

[9] "Biometrical Study of Egg Production in the Domestic Fowl. II. Seasonal Distribution of Egg Production," U. S. Dept. of Agr., B. A. I. Bull. 110, Pt. II, p. 89, 1911.

flock of 192 birds from November 1 to November 1 a total of 166.18 eggs. This value, as a matter of fact, is very close to the average production per bird of those (53) out of the 192 which were kept over for experimental purposes a second year. The corresponding total for the weighted mean annual production over the whole period is 128.86.

4. Taking the artificial year given in next to the last column of the table it is seen that in 1913–14, with 125-bird flocks, the November, December and March averages were higher than the highest made in the corresponding months during the mass-selection period, regardless of size of flock or other conditions. The April, May and July averages in 1913–14 were substantially equal to the highest made in the corresponding months under mass-selection. The highest January, February and June averages in the mass-selection period were from 1 to 2 eggs higher than the corresponding months in 1913–14. Taking the totals of the whole 9-month period compared, we have for the artificial year, made up of the highest mean monthly production under mass selection for each month regardless of the year or the flock size, *a total of 133.73 eggs per bird, while that for the single year 1913–14 is 135.82.*

Another comparison, which brings out some additional facts, is set forth in Table II. Any bird laying 18 or more eggs per month in the months November, December, January and February may certainly be regarded as a high winter producer. The proportion of such high producers in the whole flock gives valuable additional information to that furnished by the means, since the monthly egg production variation curves are distinctly skew. The

TABLE II

SHOWING PROPORTION OF FLOCK LAYING 18 OR MORE EGGS IN THE SPECIFIED MONTHS

Month	Total Flocks 1899-1907, Per Cent.	100-bird Flocks 1905–1906, Per Cent.	Flock of 1913–1914, Per Cent.
November.....	7.0	5.5	26.0
December.....	19.0	30.2	47.4
January.....	24.2	36.3	42.2
February.....	22.6	36.3	31.8

mean and median do not coincide. In Table II is shown the percentage of the whole flock laying 18 or more eggs in the months specified.

This table shows in an even more striking way than the means in Table I the marked difference between the flocks of the present time and those of the earlier years. In 1913–14 nearly half the flock laid 18 or more eggs each during December and January.

The data presented in this paper establish, I think, the following facts:

1. There is a marked difference in the average production per bird of Barred Plymouth Rock pullets of the Maine Station strain at the present time, as compared with what obtained in the earlier trap-nesting work of the Station described by Pearl and Surface (*loc. cit.*).

2. This difference is in the direction of *a substantially higher mean flock production at the present time.*

3. The increase in flock production is most pronounced in respect to winter production.

The most probable explanation of the above results appears to the writer to be that the plan of breeding now followed is more nearly in accord with the biological facts regarding the inheritance of fecundity than was the plan followed in the earlier years.

The reasons for this opinion, while not constituting complete proof of the suggested explanation, certainly make a strong body of evidence in its favor. They are, summarily stated:

(*a*) That the increases in flock productivity have been synchronous with changes in breeding practise.

(*b*) That the increases give every indication of being permanent, there having been no tendency towards a decline in flock productivity since 1908, when the simple mass selection was stopped and breeding begun on a progeny-test basis.

(*c*) That there have been no changes in management or environmental circumstances synchronous with the increases in flock production and capable of accounting for them. The hens are housed to-day in the same houses

that they were in 1904; are fed substantially the same feed, the only modification of the ration having been in the direction of one *less* stimulating to production than the one formerly used; are hatched in the same sort of incubators; reared in the same yards, etc.

(*d*) That the most marked gains have been in that cycle of production (winter laying) to which especial attention was paid in the breeding.

(*e*) That when analyzed in terms of individual matings the results obtained in egg production have been the results to be expected on the Mendelian hypothesis of the inheritance of this character earlier set forth, with only minor exceptions for which the explanation is in nearly all cases apparent.

II. An Independent Confirmation of the Sex-linkage of the Factor for High Fecundity

Besides the results with large flocks which have followed the practical application of the Mendelian hypothesis of fecundity inheritance at this Station, numerous poultrymen in various parts of the world have obtained similar results. Several instances of this sort might be cited from private correspondence. The writer has felt, however, that such cases really contributed nothing new in principle, and that therefore there was no special need of calling attention to them.

There lately appeared, however, in an English poultry paper, a note which seemed to me to be of interest on several grounds. In the first place, it is evident that the writer, Mr. E. N. Steane, is a careful observer, and an experienced poultryman. In the second place, his observations on inheritance of egg producing ability appear to be, from his point of view, entirely original and uninfluenced by any earlier work.

The parts of Mr. Steane's note[10] which are pertinent in the present connection are these:

[10] Steane, E. N., "The Production of 'Best Layers,'" *The Feathered World* (London), Vol. 52, p. 285, 1915.

My own experience, and that of many other breeders, tends to show that the birds hatched from high pedigree hens are not such prolific layers as those hatched from healthy hens of an indifferent laying strain mated to high pedigree cockerels.

For three or four seasons I bred from two-year-old white Leghorn hens of a gold-medal laying strain mated to a cockerel of equally-good descent, and the results, to my mind, were disappointing, and did not yield an adequate profit on the money spent. The pullets were less prolific than their parents, and inclined to be delicate and more or less undersized, while the percentage of fertile eggs was lessened.

Then by a lucky chance one season I had not enough eggs from a pen of Rhode Island Reds to fill up an incubator, and I made up the deficiency from a pen of good-sized healthy Leghorn hens of no particular laying strain mated to a pedigree cockerel. Practically every egg from this pen was fertile, the chickens proved strong, and the results seemed in every way satisfactory.

This, of course, led to my systematic mating of healthy, well-grown birds of indifferent laying strain to high pedigree cockerels, with very successful results. The fertility of the eggs was extremely satisfactory, the chickens turned out strong and healthy, and the pullets on arriving at maturity were highly prolific layers, each pullet averaging 200 eggs and over during the first twelve months, as against about 130 from the pullets of the high pedigree hens, many of whom also died off. In the second year the birds did equally well, the number of eggs being maintained and all being of a good size.

Later, I tried the result of mating high pedigree hens to a healthy cockerel of no special laying strain, but without success, the chickens being healthy, but the laying results much below the average, so that nothing was to be gained by further trials in that direction.

While being quite aware that many breeders do not agree with my conclusions, and that a great deal also depends on the condition and environment of the birds—prolificacy being always greatly improved by the birds having a free range, I am myself firmly convinced that such mating makes for the production of best layers. All my experiments were, of course, carried out under the same conditions in each case, the birds being kept in runs of 20 yards by 10, on well-drained, sandy soil, with a house and scratching shed attached, and fed on the same diet as that adopted in the recent laying competitions.

It is evident that Mr. Steane's experience was exactly parallel to the results of the present writer's investigations reported in earlier papers. High producing females did not transmit that quality directly to their daughters. The character is sex-linked.

The only point of difference is that noted in the second

paragraph of the quotation, and I think that the explanation of the discrepancy there is contained in the closing words of the paragraph where Mr. Steane says:

> The pullets were . . . inclined to be delicate and more or less undersized, while the percentage of fertile eggs was lessened.

This would indicate that other causes besides the breeding operations were working to bring about a poor physiological condition of the progeny, which is of course inconsistent with high productivity. Lowered fertility of eggs is one of the best indicators of reduced vitality which can be found.

We appear to have, in this case, a rather complete independent confirmation by a practical poultryman of one of the present writer's chief results in regard to the inheritance of fecundity.

III. Summary

In this paper it has been shown that:

1. There is a marked difference in average egg production per bird of Barred Plymouth Rock pullets of the Maine Station strain at the present time as compared with what obtained during the period of simple mass-selection for this character.

2. This difference is in the direction of a substantially higher mean production at the present time, when tested on flocks of large size.

3. The increase in flock average productivity is most pronounced in respect to winter production, which is the laying cycle to which especial attention has been given in the breeding.

4. The cause of this increase in flock productivity appears, with a degree of probability which is very high and amounts nearly to certainty, to be that the method of breeding the stock now followed is more closely in accord with the mode of inheritance of fecundity than was the simple mass-selection practised in the earlier period.

5. The result announced in earlier papers that high fecundity is a sex-linked character, for which the female is heterozygous, has been confirmed by practical poultrymen in their breeding operations.